

The *Edwardsia*-stage of the Actinian *Lebrunia*, and the Formation of the Gastro-cœlomic Cavity. By J. E. DUERDEN, Assoc. Roy. Coll. Sci. (London), Curator of the Museum of the Institute of Jamaica. (Communicated by Prof. HOWES, Sec. Linn. Soc.)

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(PLATES 18 & 19.)

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DURING the temporary establishment in November, 1898, of a marine biological laboratory at Bluefields*, Jamaica, in connection with the Institute of Jamaica, several specimens of a *Lebrunia* were found in the act of extruding larvæ. An examination of these, while in the living condition and when sectionized, discloses, amongst other characters, some very exceptional features in the development of the tentacles, and in the formation of the gastro-cœlomic cavity of the adult. I am also able to add, by way of comparison, a few facts in connection with the freshly-extruded larvæ of *Aulactinia stelloides*, McMurrich.

I. SYSTEMATIC.

The specific determination of the first-mentioned Actinian calls for a few remarks. It is a small form which occurs in

* Bluefields is the name given to a property, formerly a sugar estate, on the south-west coast of Jamaica, rendered classic to local naturalists as the residence of Philip Henry Gosse, F.R.S., during his collecting trip of eighteen months, from 1844-46. The principal features of its natural history, and those of Bluefields Bay, are most vividly portrayed in Gosse's work: 'A Naturalist's Sojourn in Jamaica' (London, 1851).

considerable numbers all round the island, at a depth of two or more feet, within crevices of coral-rock. In "The Actinaria around Jamaica" (1898), I identified it as the *Hoplophoria coralligena* of H. V. Wilson (1890), transferring it at the same time to the genus *Lebrunia*.

The chief characteristic of this genus is the presence of four to eight dichotomously branched outgrowths (pseudo-tentacles) from the uppermost region of the column. They occur immediately external to the tentacles, and usually bear spheroidal batteries of nematocysts.

Dr. Wilson's species was founded upon a single specimen, about 2 mm. in diameter, discovered in a hole in the coral-rock on the Bahama reefs. There appears to be the closest external resemblance between the Jamaican and the Bahaman examples; and anatomical and histological examination supports this, even to the peculiar forms of the nematocysts, and an exceptional arrangement in separate bands of the endodermal muscle of the columnar outgrowths. Comparisons made with the Bahaman *Lebrunia* described by Prof. McMurrich (1889), and with the Jamaican representatives of the genus, also show a close agreement; hence, in the paper above mentioned, I stated (p. 457) that "it is possible that it may be but a young form of *L. neglecta*."

When I first came upon the Jamaican polyps specimens were sent to Prof. Wilson for his opinion as to their similarity with his species, and he obligingly writes as follows:—"In your preserved specimens the pseudo-tentacles have a noticeably different appearance from those of my single specimen. The white nettle-batteries so conspicuous in my specimen are not obvious in yours. I note though that you find them conspicuously outlined in the living animal. The pseudo-tentacles in your specimens are much larger and more flaccid than in mine. All slight and variable points of difference. I make no doubt they are the same provided your sectional study shows the internal anatomy and histology to be alike in your specimens and in mine."

Prof. McMurrich (1893, p. 133) has expressed the opinion that Wilson's species is identical with *Viatrice globulifera*, Duchassaing. But in the description and figures given by Duchassaing and Michelotti (1860) of this Guadeloupe species the columnar

outgrowths are very numerous and vesicle-like, and the polyps float freely, characters never met with in the form under consideration.

Within the past year, Prof. A. E. Verrill (1898), without experience of either form, has cast doubts upon the identity of the Jamaican specimen with the true *Hopliphoria coralligens*, and also with the conclusion that it may be but a young form of *Lebrunia*.

From the above facts, however, no other conclusion than that it is identical with Wilson's species seems possible, and in the fuller description yet to be published I hope to show its agreement with the Jamaican *Lebrunia*. Meanwhile, it will be sufficient to refer to it as *Lebrunia coralligens* (H. V. Wilson).

The adult polyps are hermaphrodite. Ova and spermata occur in considerable numbers closely associated in the same mesentery.

II. EXTERNAL CHARACTERS.

In living polyps the larvæ were to be seen through the somewhat transparent tissues of the parent moving about within the cœlenteron, and especially within the tentacular cavities. As many as five were contained within a single tentacle.

So far as could be observed, they possessed little or no motion of their own, but allowed themselves to be carried along by the circulation of the cœlenteric fluid. By a peculiar jerking action of the adult three or four larvæ at a time would be shot out through the mouth for some distance, and then sink to the bottom of the vessel. Here they would lie unattached for some time in any position, though usually on their side. Afterwards slow movements, both translatory and rotatory, would commence, but these at no stage became pronounced. Individuals might come to rest at apparently any point of their surface and again commence their swimming movements.

When first extruded the larvæ measured about 1 mm. in length and were of a pyriform shape (Pl. 18. fig. 1), divided by shallow grooves into eight, nearly equal, longitudinal regions. Sometimes they would take the form represented in fig. 2, or become short and cake-like as in fig. 3. Viewed along the edge, the colourless ectoderm was easily distinguished from the endoderm, the latter dark brown from the presence of numerous zooxanthellæ. In

surface view eight longitudinal darker and lighter areas were clearly marked, the coloured areas corresponding with the mesenterial chambers, and the colourless with the line of origin of the mesenteries. The mouth was already indicated at the broader end as a slightly depressed, small, circular aperture; the aboral end was narrow and rounded (Pl. 18. fig. 4).

The perioral ectoderm differed from the remainder of the outer layer in being dark brown in colour, owing to the inclusion of zooxanthellæ. Some of these apparently worked their way out from the ectodermal cells and adhered superficially, or, in other cases, became free. Their presence at various heights in this restricted region is also revealed in sections.

Contrary to the usual condition in the Actiniaria, the ciliation was uniform over the whole surface. The larvæ progressed with the narrower, aboral end foremost, and also attached themselves finally by this extremity. Even during the first day their power of adherence to the bottom and sides of the vessel was considerable, sufficient to resist a strong current of water from a pipette.

The description given applies to each of the larvæ extruded, all having apparently reached a similar stage of development. The subsequent growth, so far as followed, was likewise the same in each. No earlier stage could be seen through the transparent tissues of the adult, and when a polyp was cut in halves none floated out. It is evident, then, that in *Lebrunia*, as appears to be also the rule in many other Zoantharia, the ova are ripened and the embryos develop and are expelled in batches; for, were it otherwise, different stages would be represented within the gastro-cœlomic cavity at one and the same time.

Such, however, is not always the case. While at Port Antonio, on the north-east coast of Jamaica, working in the temporary Marine Laboratory established there in 1897, by the Johns Hopkins University, specimens of *Aulactinia stelloides*, McMur., were collected, and from these larvæ were also being set free. Here the individuals, each with an aboral tuft of longer, less mobile cilia, were thrown out from the internal cavity of the adult by the same jerking motion as in *Lebrunia*; but many different stages were represented in one parturition, and a like variety of phases could be observed through the partly transparent tissues. Minute planulæ, showing what seemed to be the beginning of an invagination, would appear along with larvæ possessed of eight,

strongly marked ridges and furrows, and even, in a few cases, with as many as six or eight tentacles already developed. Only the younger stages here continued to swim about; the older straightway fixed themselves to the bottom of the vessel by means of a flattened basal disc.

Development of Tentacles.

Within the first twenty-four hours the larvæ of *Lebrunia* settled down, and indications of the future tentacles were presented by a slight bulging from each of the eight intermesenterial areas. These were at first rounded as in Pl. 18. fig. 4 *a*, but, on becoming larger, narrowed a little as in figs. 5 & 6.

From the first a distinction into two alternating groups of four was obvious, one series being slightly larger than the other, though all constituted only one cycle.

Many of the adult polyps are characterized by the occurrence of superficial, opaque white areas on the oral aspect of the tentacles, much more pronounced later on the columnar outgrowths. The opacity on the tentacles is found to appear at the earliest stages, at first on the four larger prominences and later on the four smaller.

For some time it was not possible to recognize any difference in size amongst the members of any one group of tentacles, the disc presenting a perfect tetrameral radial symmetry. Later, one tentacle became slightly larger than the rest. Following the conventional nomenclature proposed by Kölliker and now usually adopted, this will be the dorsal tentacle; or, in the more morphological terminology of Haddon (1889), the sulcular. The tentacle opposite will be the ventral, or sulcar, and the plane in which they are enclosed the dorso-ventral or sulculo-sulcar. In the further increase in size the dorso-lateral pair of tentacles, that is the tentacle on each side of the dorsal tentacle, remained a little behind the ventro-lateral pair—these four forming the smaller series in the earlier stage.

The larva thus changed from its primary condition of radial symmetry to a decided bilateral form, the sagittal plane passing through the large dorsal and the ventral tentacles.

At the expiration of two or three days the larvæ had reached the stage represented by fig. 7 (Pl. 18). The aboral end is now flattened and disc-like, and even slightly larger in diameter than

the column; the latter has narrowed and become cylindrical, but still shows only eight alternating dark and light areas. The eight tentacles are finger-shaped, rounded at their free extremity, and able to move about, but, as in the adult, are incapable of retraction. The oral disc is flattened, its ectoderm still retains the zooxanthellæ, and the mouth is circular or oval-shaped.

The dorsal tentacle is a little stouter and longer than the others, and the originally smaller ventro-lateral tentacles are now practically of the same size as the three remaining members of the first series, *i. e.*, the ventral tentacle and the two median laterals. The dorso-laterals, however, have lagged considerably behind in their development. At their base they are also pushed out slightly further from the disc than the other six, which now are beginning to form a cycle by themselves.

The larvæ are clearly sensitive to the action of light. When settling they would select the under surface or a crevice in any fragment of coral-rock placed in the vessel, and if the fragment were turned over would detach themselves and move to some less exposed spot. The adults usually live associated in shady crevices, the pseudo-tentacles and tentacles protruding as a delicate fringe. During the ordeal of examination under the strong tropical light, the larvæ would slowly assume a more or less collapsed aspect, their healthy inflated appearance returning after being shaded for some time. This behaviour towards light I find also to be very general amongst adult Actinaria and Madreporaria.

Several examples were kept alive for six or seven days, but none passed beyond the stage represented in fig. 7. No trace was presented of the pseudo-tentacles. The development of the larvæ after extrusion was at first very rapid, the stage last mentioned being reached within forty-eight hours. The only external alteration during the next four or five days was a slight increase in dimension of all the parts, without any indication of additional tentacles or mesenteries. Unfortunately, circumstances did not permit of further observation.

The chief external characters, other than that of size, in which the adults differ from the oldest larvæ are: (1) the presence of several cycles of entacmæous tentacles, arranged in the formula 6, 6, 12, 24, 48, the members of any cycle being equal; and (2) the six (normally) large branching "pseudo-tentacles,"

arising from the most distal region of the column and bearing spheroidal batteries of nematocysts. The mouth, instead of being circular, is very long and narrow.

From what we already know of the development of other Zoantharia, the hexamerous character of the adult tentacles is in most cases derived from the readjustment of primary tentacles of different sizes and origin. Thus, already in the larvæ the first cycle of six is indicated, constituted of the four larger of the eight primary tentacles and two of the smaller. The remaining two will probably form one of the pairs of the second cycle of six tentacles alternating with the first, in which case it is obvious that the second cycle will be composed of individuals of a very different order of development.

As regards the tentacles, then, *Lebrunia coralligena* passes through three very distinct stages:—(1) a tetramerous radial symmetry, with four large and four small tentacles; (2) a bilateral symmetry of the same parts, six tentacles being nearly equal and forming one cycle, and two remaining smaller and outside the others; (3) the approximate hexamerous radial symmetry of the adult, with numerous alternating entacmæous cycles.

The simultaneous appearance and tetramerous radial arrangement of the tentacles here described in the first stage is in marked contrast with what is known of the tentacular development of the Zoantharia generally.

Comparatively few observations on the order of appearance of the tentacles have, however, been recorded. One of the fullest and best is the well-known account given by Prof. de Lacaze-Duthiers of the growth of *Actinia equina*, and supplemented by observations on other species. Not having the original monograph for reference, for what follows I am dependent upon the many figures and details reproduced by Prof. E. L. Mark in his "Selections from Embryological Monographs" (1884), and by Prof. A. C. Haddon in the concluding portion of his "Revision of the British Actiniæ" (1889). From these it appears that the dorsal tentacle is the first to arise, and for a long time this predominates over the others. The octoradiate stage quickly supervenes, the median lateral tentacles being the next largest to the dorsal, and the ventral protuberance one of the smallest. The great difference in size between the dorsal and ventral

tentacles gives a strongly bilateral character to the larva, exceeding that ever exhibited by *Lebrunia*. The latter seems more closely to resemble *Bunodes verrucosa* (*B. gemmacea*), in which Lacaze-Duthiers found the octoradiate stage to be of longer duration.

The succeeding stages, showing the manner in which from tentacles of heterogeneous origin the hexamerous cycles of the adult are obtained, do not now concern us, except to say that in all probability *Lebrunia* passes through similar phases.

Aulactinia larvæ afford somewhat similar results. I obtained freshly-extruded examples with only six tentacles developed, one smaller and one larger tentacle on each side of the dorso-ventral tentacles. Others, again, show eight tentacles; of the new pair one arises on each side of the dorsal tentacle.

Among the Ceriantidæ McMurrich (1891 *a*) and E. van Beneden (1891), in the same year, have confirmed the previous observations of Agassiz and Kowalewsky, that the first six tentacles arise in lateral pairs, and that then a single median tentacle—the sulcar—appears. No radial phase is ever assumed in any of these earliest stages yet described. Prof. G. von Koch (1897, p. 759), however, in the numerous larvæ of *Caryophyllia cyathus* which he had under observation, found the first twelve tentacles to appear apparently at one and the same time, six larger alternating with six smaller, just as in the adult. In one case they developed in pairs, the dorso-ventral pair appearing first.

The relation of the different tentacles to the internal mesenterial spaces is described later (p. 297).

III. INTERNAL ANATOMY AND HISTOLOGY.

In all about thirty extruded larvæ were obtained, and reared to different stages within the course of a week. Among a number of adults collected in 1896, at the Port Royal Cays, a polyp with its interior crowded with preserved larvæ was also detected. Cutting this across upwards of thirty examples floated out freely, or were easily separated from among the tissues. These were devoid of tentacles, and internally all presented precisely the same stage of development—a stage, it will be seen later, slightly in advance of that exhibited by the youngest of the expelled larvæ. In speaking, therefore, of early

and late larvæ, I refer to phases reached in the development, independently of whether the examples were or were not extruded. Practically all the material was utilized for purposes of study.

Succinctly the general facts of the anatomy and histology are as follows:—

The ectoderm is a thick layer with the constituent elements—ciliated supporting cells, nematocysts in all stages of development, gland-cells, and nerve-elements—well differentiated. The supporting lamella contains isolated cells, and a definite, though very weak, musculature is already formed on its inner surface, its fibres arranged in a circular manner.

Eight mesenteries are present and extend the whole length of the larva; in the upper stomodæal region they are all perfect and arranged tetramerally*.

The stomodæum at first is a very short, strongly ciliated, rounded tube, without any external aperture. Internally it communicates with four radiating canals, which are connected with two sinuses, and these terminate in a system of inter-

* Such a stage in which only eight perfect mesenteries are present, and in which no further numerical increase takes place for some time, has been found to be very constant in the development of the Zoantharia. The mesenteries are those of the first four pairs, and consist of two lateral pairs and two median pairs—the directives. The retractor muscles on the two lateral pairs occur on the face of the mesenteries turned towards one pair of the directives, which, following the terminology of Haddon, is the sulcar or ventral. The other pair of directives is the sulcular or dorsal, and in these the retractor muscles are likewise on the face directed towards the sulcar aspect of the polyp.

The pair of lateral mesenteries next the sulcar end—sulco-lateral—are the first to appear in the embryo; then, in the majority of cases, the lateral pair next the sulcular end—sulculo-lateral; the sulcar directives constitute the third pair, and the sulcular the fourth in the order of development.

Lacaze-Duthiers first recognized the octoradiate condition as one of the resting stages in the development of the Actinæ. Haddon (1889) described it as the third stage of mesenterial development, at the same time realizing its phylogenetic importance and similarity to the permanent condition in the *Edwardsiæ*; McMurrich (1889) obtained it in *Aulactinia stelloides*, and later in others, and applied the term "Edwardsia-stage," an apt designation since adopted by all writers on the subject. The researches of these authors, and of H. V. Wilson, Boveri, van Beneden, G. von Koch, and others, demonstrate that the phase is repeated in the ontogeny of such diverse groups as the Cerianthæ, Zoanthæ, Hexactinæ, and the Madreporaria.

mesenterial and mesenterial spaces. The spaces throughout have a distinct ciliated limiting layer, in continuity with the lining of the stomodæum. Otherwise the whole of the interior is filled with a vacuolated, undifferentiated tissue, provided with nuclei and zooxanthellæ, but devoid of yolk. Such a larva may therefore be regarded as a nearly solid mass of cells.

Between the earliest larvæ and the latest, changes of great significance have been effected, in addition to those involved in the production of the tentacles.

The middle vacuolated tissue has broken down and a gastro-cœlomic cavity of the usual Cœlenterate type is in process of formation; into this the stomodæum, now provided with an oral aperture, depends and opens directly. The primary spaces are in process of giving rise to the mesenterial chambers of the adult.

One pair of the original eight mesenteries—the sulco-lateral—remains connected with the stomodæum longer than the rest, and each of the pair bears mesenterial filaments in direct continuity with the stomodæal lining. Only the median streak is as yet developed.

Of the many expelled larvæ secured, only two or three retain the solid phase in its perfect condition, with the stomodæum and its diverticula intact. The remainder, including the specimens preserved within the body of the adult, have passed into the second stage in which the middle tissue is becoming disorganized.

The different structures will now be described in greater detail.

1. *Ectoderm.*

The ectoderm is an exceptionally broad layer, uniformly ciliated throughout, with its free margin very pronounced in sections stained in borax-carminé or hæmatoxylin (Pl. 18. fig. 8). This latter character is due to the occurrence of a very delicate rectangular enlargement at the base of each cilium; the closeness of these and the readiness with which they take up colouring-matter produce a strong delimitation from the rest of the layer. The Hertwigs (1879, Taf. iii. figs. 5-8) figure a similar appearance at the edge of the ciliated ectoderm of the external surface and stomodæum of *Anthea cereus*.

Most of the nuclei of the various cellular constituents are arranged in a broad zone a little within the periphery, but a few

appear in the deeper regions and as far as the mesoglœa. A peripheral zone of the ectoderm is nearly colourless, being constituted mainly of the distal portions of the extremely long supporting cells, unicellular glands with clear contents, and a few gland-cells with fine granular contents. These last stand out very distinctly in sections stained with indigo-carmin. The nuclei of the principal zone are oval and closely arranged, staining not nearly so intensely as those of the stomodæum and mesenterial filaments. The inner nuclei are rounded and much more scattered; some approach the supporting lamella, and others appear partly or even entirely included within it. The mesoglœa of the adult polyps contains numerous isolated cells equally distributed throughout, and there is little doubt that these are derived both from the ectoderm and the endoderm. For in the larvæ nuclei in similar positions to those of the ectoderm already referred to also appear on the internal side, and the thin lamella of the mesenteries also displays included cells. Both in longitudinal and transverse sections a very delicate layer of nerve-fibrils can be distinguished next the mesoglœa, much more obvious at the narrower end (Pl. 19. fig. 21). Maceration-preparations of such delicate material in the preserved condition did not yield good results, but I was able in some instances to distinguish the usual nerve-fibrils of the sensory cells.

No distinct evidence of muscular fibrils occurs on the ectodermal side, but in longitudinal sections such can be recognized on the inner border of the mesoglœa of all but the youngest larvæ (fig. 21).

The nematocysts are of two kinds. A long narrow form extends almost across the layer and is distributed throughout the ectoderm, even as far as the aboral region. They particularly crowd the tentacular area. On maceration, a very small oval form is also obtained, often with the nucleus of the cnidoblast still connected. These are not early stages of the larger variety, as the developing forms of these latter are very conspicuous objects.

The large nematocysts are extremely thin-walled, nearly transparent, and usually only a central, nearly straight, more highly refractive axis can be distinguished, extending from one end to near the other. In some conditions the presence of a very delicate, closely spiral thread can be observed in addition. Nearly

all my preparations reveal the curious fact that, in the process of sectionizing, many of the nematocysts become dislodged from the ectoderm, and dragged to what would be the margin of the paraffin block, without causing any apparent injury to the other elements.

Here and there throughout the layer, more numerous in the tentacular region, occur nematocysts in various stages of development. They are at once recognized by their homogeneous and deeply-staining character. In this respect they contrast strongly with the mature forms, the walls of which are not affected by borax-carminé, though they become slightly blue in indigo-carminé. Most of the nematocysts originate in the deeper parts of the layer, and, at first, are a little concave or irregular in outline, and arranged obliquely or even tangentially to the surface. When mature they extend as far as the external surface and are disposed vertically. Both the wall and the axis take up the stain in the nearly ripe condition, and in transverse sections of earlier stages the contents are homogeneous in the middle but granular towards the margin.

Around the aboral end the ectoderm is of a very different character from elsewhere (Pl. 19. fig. 21). The periphery is crowded with small nematocysts, provided with a very distinct spiral thread; large, pyriform, deeply-staining bodies, perhaps glandular, occur more internally, and towards the supporting lamella the nervous layer is exceptionally well-developed. Such a special development of the protective, sensory, and probably glandular elements of the layer is, no doubt, in some way associated with the fact that in the free active stage this end of the larva is foremost, and that it is by this that it ultimately attaches itself. McMurrich (1891, p. 317, pl. xiii. fig. 13) describes and figures a somewhat similar exaggerated development of the nervous layer in the embryo of *Rhodactis*.

As already mentioned amongst the external characters, and contrary to the usual condition in adult Zoantharia, the ectoderm contains zooxanthellæ, restricted, however, to the central area of the oral disc. In the oldest larvæ they occur throughout the thickness of the discal ectoderm, but none remain in the adult polyps.

Compared in other respects with the ectoderm of the adult, there is a great increase in the latter in the proportion of uni-

cellular mucous glands with nearly clear contents; cilia are not obvious in material preserved in the same manner and at the same time as the larvæ; and practically no increase in thickness of the layer has taken place. A weak ectodermal musculature occurs on the tentacles, oral disc, and uppermost part of the adult column.

The nematocysts of the columnar outgrowths (pseudotentacles) in the adult are of a different kind from those already described, being oval and much shorter, with a loose, irregular spiral thread.

2. *The Archenteron and Formation of the Œsophagus.*

It is remarkable that in all the larvæ taken from the preserved adult there is no external aperture (Pl. 19. fig. 21). This is also the case with the extruded larvæ at the time they are set free (fig. 15), but a mouth is established very early after as a result of an infolding of the discal ectoderm. From this it would seem that the structure in *Lebrunia*, hitherto spoken of as the stomodæum, must, prior to its communication with the exterior, be regarded as an endodermal-lined archenteron, for there are important morphological differences between its earliest and latest conditions.

If the discovery of earlier stages should prove that at the blastula-stage of development a primary archenteric invagination is established, then its external opening—the blastopore—has become closed, and only later another aperture is produced, over evidently the same spot, and this persists as the mouth. The entire tube thus formed, partly from the archenteron and partly from the secondary invagination, persists as the œsophagus of the adult.

Fortunately, a fairly complete series of preparations has been obtained showing the different stages in this latter transformation. In the non-extruded larvæ (fig. 21) the blind archenteron is easily distinguished by means of its deeply-staining lining; outwardly it extends as far as the external ectoderm, its narrow lumen recognizable all the way. The supporting lamella is seen to be invaginated for a considerable distance, but does not extend transversely. The ectodermal cells immediately over the archenteron are rather loosely arranged, and zooxanthellæ occur amongst them. It appears as if all that is needed to bring about

the adult condition is for the archenteron to extend itself a little, and thus set up a communication with the exterior.

Vertical sections of one of the freshly-expelled larvæ prove that this is apparently not the case, but that to form the adult oral aperture and œsophagus a distinct invagination of the superficial ectoderm takes place. This is very distinctly shown in the actual sections represented in Pl. 18. figs. 9 to 11, taken from a series of vertical sections through the archenteric region of an extruded larva, before disintegration of the central tissue has commenced. In the particular larva the transverse, separating tissue of the invagination has evidently just broken through, establishing communication, but the lateral walls still indicate how the whole process has been carried out.

Fig. 9 is from a tangential section through the wall of the archenteron and the invaginated region above. The ectoderm directed inwardly differs much in character from that beyond; zooxanthellæ are absent, and a greater number of deeply-staining nuclei cause it to stand out very distinctly. A straight, ciliated edge indicates the free surface of the floor of the ectoderm; while a middle region below, nearly devoid of nuclei, represents where the lower surface of the invaginated end has come into contact with the expanded upper end of the archenteron.

The free margin of the wall of the latter, bordering on the flattened archenteric or cœlomic chamber, is also very strongly ciliated. The floor of this chamber is at this stage entire and sharply defined; the limiting layer is ciliated and contains abundant nuclei, which easily distinguish it from the vacuolated tissue below and around. To the right the floor is continued further into the diverticular system (*cf.* left side of fig. 15, Pl. 19).

Fig. 10 (Pl. 18) is from another tangential section, but nearer the lumen than the former. An external aperture is now presented, the outer ectoderm being seen as an inturned layer. The floor of the invagination is dome-shaped and extends some distance laterally. The area of its union with the roof of the archenteric cavity can even yet be distinguished owing to its diminished number of nuclei. The central cœlomic space is still flattened, but the preparation does not permit of the lateral extensions being followed.

Fig. 11 represents a section through the actual lumen. The central tissue, consisting of the floor of the ectodermal invagina-

tion and the roof of the archenteron, is now absorbed or broken down. The floor of the invagination is still represented laterally by the very marked indentation on each side, the actual point of union of the two layers being in the neighbourhood of the lower edge. Neither in this section nor in any of the later stages can the actual union of the invaginated ectoderm and the archenteric endoderm be recognized by any histological difference. The lumen throughout is now much wider than hitherto, but soon narrows again.

In all the other extruded polyps of which I possess vertical sections the stage reached is later than the above; the stomodæum has straight walls, and no indication is afforded of any double origin of its lining.

Strictly, then, only the upper, ectodermal-lined region of the gastric funnel in *Lebrunia* is homologous with the stomodæum or fore-gut of the Enterocœla; the lower region, lined with archenteric endoderm, is equivalent to a portion of the mesenteron or mid-gut of the higher Metazoa. While such conditions as those revealed in fig. 21 (Pl. 19), where the archenteric endoderm is in absolute continuity with the filamental tissue, strongly suggest that the mesenterial filaments along the free edge of the mesenteries are but the banded continuations of the enteron.

On account of the seeming double origin of the gullet in *Lebrunia*, the term œsophagus is preferable to the term stomodæum usually employed in Actinozoan literature for this structure. The former, as used in the Enterocœla, implies merely the first portion of the adult gastric canal, without any reference to the embryonic origin of its lining, though usually it possesses both an ectodermal and an endodermal portion; while the latter is the term employed to designate the extent of the invaginated ectodermal lining of the gastric canal. The justification for the employment of stomodæum in the adult Actinozoon rests upon the fact that, in general, the lining of the gullet is wholly derived from a primary ectodermal inturning, but it is obvious, from the details just given, that this may not always be the case.

We may thus summarize the formation of the oral aperture and œsophagus:—An invagination of the external ectoderm takes place directly over the outer extremity of the archenteric tube, and at the same time the layer undergoes a considerable

histological alteration. Its floor presses upon the blind end of the archenteron, and the result is a mutual flattening, leading to a convexity in the former and a considerable lateral extension in each. The two ends ultimately break down in the middle, and a communication between the interior and exterior is thereby established. The lateral walls of the invaginated ectoderm and of the archenteric endoderm form the lining of the adult œsophagus.

Once the œsophagus is fully established, the lumen at first is extremely small, and circular in transverse section. Even in the older larvæ the outline may be circular in some places, but oval in others, the longer axis always corresponding with the sulco-sulcular axis of the mesenteries. No histological change suggestive of a gonidial groove ever takes place at either end, a condition not to be expected, as gonidial grooves are not present in the adult.

The lining is more strongly ciliated than that of the columnar ectoderm; indeed, it is the most strongly ciliated layer of the whole larva. As in the column a small, deeply-staining enlargement occurs at the base of each cilium.

The nuclear zone is very pronounced; the nuclei are oval, closely arranged, and stain a brilliant red in carmine. Clear gland-cells appear to be absent, but granular gland-cells occur here and there, and long, narrow nematocysts similar to those of the column. The mesogloea is extremely thin. Only in some of the most favourable sections of the older larvæ can suggestions of a nervous layer be observed, though this is very pronounced in the adult.

Aborally the œsophagus opens directly into the gastro-cœlomic cavity. In perfectly horizontal sections the sulcar and sulcular ends terminate at about the same level. At the inner extremity a slight reflection of the strongly-nucleated lining takes place all round, so that in transverse sections at this point the latter appears cut through twice (Pl. 19. fig. 18). The reflected portion is more or less connected with the mesenterial filaments at their origin; it is further discussed under the section Mesenterial Filaments.

In the adult polyp the œsophagus is greatly elongated transversely, so that it stretches nearly across the cœlenteron, the directive mesenteries being much shorter than the four lateral

pairs. Gonidial grooves are absent. An exceptionally well-developed nervous layer occurs, without any accompaniment of muscular fibres, and granular gland-cells are numerous.

3. *Larval Cœlomic Spaces and Formation of the Gastro-cœlomic Cavity.*

Transverse sections through the upper archenteric region of the youngest larvæ, before any disorganization of the internal tissue has commenced, reveal very narrow, isolated, slit-like spaces within the intermesenterial, parenchymatous tissue, one near the middle of each face of a mesentery (Pl. 18. fig. 12, *d, e, f*). A little lower the two within each chamber become connected by a transverse channel, and still lower only a single median cavity occurs in each radial division (fig. 12, *g, h, c*), the lateral boundaries always remaining close to the face of the two enclosing mesenteries.

Approaching the inner termination of the archenteron, where three pairs of the mesenteries have become free, each cavity broadens somewhat, and communication is established between the five chambers on the dorsal or sulcular side of the sulco-lateral mesenteries, and also between the three on the ventral or sulcar side, two distinct sinuses being thus formed (fig. 13). The successive steps in the sinus formation, following the disappearance of the centripetal parts of the mesenteries, are shown in fig. 12, in connection with the intermesenterial spaces *b, a, h*. In this particular instance the sulcar mesenteries are the first to lose their connection with the archenteron and permit of communication.

Fig. 13 represents the arrangement of the various cavities at the inner end of the archenteron. It delineates the details observed in several sections of a polyp which happened to be cut slightly obliquely to the vertical axis. The archenteric tube terminates in four canals, one of which communicates with the sulcar sinus and three with the sulcular sinus. Were the sulco-lateral pair of mesenteries developed only to the same extent as the others, it is obvious that a complete circumferential sinus would be established.

For a short distance below, the two sinuses remain distinct, but later become sub-divided into eight V-shaped chambers, associated with the free edges of the mesenteries.

The various stages leading to this are represented in fig. 14, taken from a single oblique section in which the upper part is more aboral than the lower. Traces of the two sinuses are still seen in the latter region, and on the right side the last evidence of the sulcar canal; while, in the upper half of the figure, the V-shaped canals, embracing the free edge of the mesenteries, are distinct. This latter condition holds for all the mesenteries as far as their lower termination.

A vertical section, such as would be obtained along the line $x-y$ in fig. 12, is represented in fig. 15 (Pl. 19), taken from one of the youngest larvæ. The archenteron opens into a shallow central chamber, from which two canals radiate, one to the left and the other to the right. Histologically the floor of the chamber differs considerably from the undifferentiated tissue below, more nearly resembling the endodermal lining of the archenteron. Vertical sections of one early larva show this chambered region very distinctly; some (figs. 10, 11) with the right side terminating blindly, and others (fig. 9) with a canal-like continuation. The precise outline of the diverticulum to the left in fig. 15 is largely deduced from the various transverse sections, as only isolated parts are recognizable in the actual vertical preparations.

The boundary of all the canals and spaces is regular and smooth, and cilia can be distinguished, not, however, so thickly disposed as in the archenteron. Everywhere at its origin the limiting layer is in continuity with the archenteric lining, and throughout bears a close resemblance to it. The cells constituting it are more or less separable from the rounded, vacuolated cells below, being columnar and filled with finely granular, protoplasmic contents; oval nuclei are much more numerous than elsewhere, and are arranged in a somewhat regular layer.

Throughout the best-preserved larvæ the margins stand out prominently in sections stained in borax-carminé, owing to the greater abundance of nuclei which readily take up the stain.

In sections the vacuolated tissue, both central and peripheral, most closely recalls the parenchymatous tissue of plants. The cells are somewhat polygonal in outline, their boundaries being extremely thin, and the contents have almost entirely disappeared. Here and there a nucleus occurs applied to the walls, and zooxanthellæ are distributed throughout. No objects at all suggestive of yolk-granules are present in any of the stages. The tissue

probably shares in the formation of the muscular system, for in connection with it delicate fibrils are recognizable on the column-wall (fig. 21) and mesenteries (fig. 16).

The limiting cells next the supporting lamella of the column-wall are not arranged in any definite layer, and appear to differ in no respect from those more central.

Nuclei sometimes occur here more abundantly than elsewhere, and often in a similar manner along the two faces of the mesenteries. They are probably connected with the formation of the mesogloea, and some seem to become included within it.

To recapitulate: The archenteron terminates internally in a small central cavity, from which four canals radiate and open into two circumferential sinuses, extending slightly above and below. In the middle archenteric region of the larvæ the sinuses subdivide into eight distinct chambers, one for each radial division, and ultimately each of these terminates in two cornua, sixteen in all. Below the archenteric region the sinuses terminate in eight V-shaped canals, each of which is formed, as it were, by the union of two cornua from adjacent mesenterial spaces. Owing to this the lower terminal chambers are mesenterial in position, while the upper must necessarily be intermesenterial. A ciliated limiting layer closely resembling in structure, and in absolute continuity with, the archenteric endoderm is throughout easily distinguished from the general mass of undifferentiated tissue. This system of spaces I regard as a larval cœlome or body-cavity arising in connection with an archenteron, but not cut off from it.

Instead of representing a definite and independent system of larval cœlomic diverticula, it may be urged that the spaces are merely the initial clefts in the disorganization of the solid interior, to be completed later. Against this I would point out that the canals and spaces all exhibit the distinct limiting layer, very different from anything to be associated with disintegrating tissue; and that in the intermediate larvæ, where the process can be followed, the breaking down of the cells commences just below the internal opening of the archenteron, attacking first the central mass. It is not until very late that any alteration takes place in the more proximal and distal spaces. And further, there is evidence that the greater part of the limiting layer becomes the unilaminar epithelium of the adult cavity. It is not disintegrated.

The internal appearances of the various regions of a later larva, one in which the disorganization of the central tissue is in progress, though the mouth is not formed, are represented in Pl. 19. figs. 16-21. The first five are taken from actual sections of one of the non-extruded polyps, while fig. 21 is constructed so as to represent what would be obtained along the lines I-x, x-I in fig. 19. As a matter of fact, however, fig. 21 was obtained almost entirely from a single vertical section. The sections from which figs. 16-20 are taken would be along the lines 1-1, 2-2, 3-3, 4-4, 5-5 respectively of fig. 21.

Fig. 16 passes through the upper region of the archenteron, just below the sections showing the sixteen separate slit-like cornua. The spaces are very regular and crescent-shaped. Fig. 17 approaches the inner termination of the archenteron, only the sulco-lateral pair of mesenteries being still attached to the latter. The sulcular and sulcar sinuses are established, but neither here nor lower is there any trace of the archenteron dividing into canals. Four regions are indicated on its cœlomic epithelium, in which the deeply-staining tissue in continuity with the archenteric lining is becoming concentrated. The two in the sulcar sinus are distinct, but the sulcular pair are nearly united, though more distinct in sections above.

The appearance of the terminal walls of the tube alone is represented in fig. 18. The deeply-staining endoderm is cut through twice as a result of its reflection (*cf.* fig. 21, 3-3). The reflected moiety is now separated into two parts by the connection of the sulco-lateral mesenteries, which are seen to extend as far as the actual termination. The same tissue, developed to a much less degree, can also be traced along the margin of the mesenterial epithelium.

The next figure (fig. 19) is from a section below the archenteron, and shows the larger, filament-bearing, sulco-lateral mesenteries, and relics of the disorganized central tissue, in the gastro-cœlomic cavity now in progress of formation. Comparing this with figures 9-11 of the earlier stage, it will be seen that the portion to disintegrate is that central to the two sinuses, including both the limiting layer and the enclosed mass of parenchymatous tissue.

The peripheral portion has not yet commenced the changes resulting in the unilaminar epithelium of the adult; it is still

many cells in thickness, and its margin is strongly ciliated and nucleated.

In sections for some distance below the middle of the larva the mesenteries are all of the same size, and there is a large central cavity, but towards the aboral region the cavity is again nearly obliterated. The details here represented indicate the stages followed during the progress of disintegration. The vertical section in fig. 21 will assist in making the relations described a little clearer.

From these details it is evident that the only actual disintegration as yet is that involving the central tissue internal to the two circumferential sinuses, and extending to the aboral region and some distance within the œsophageal region. In the expelled larvæ the process, like that of the formation of the oral aperture, was set up immediately after liberation, and must have proceeded rapidly; for in only three specimens was I able to obtain the stage in which the centre is still solid and the diverticula distinct throughout. On the other hand, it is well on the way in the non-extruded larvæ, which are still devoid of any external opening.

Remains of the primary solid condition continue to be represented for some time peripherally, by an enormously thickened ridge of parenchymatous tissue, connected with the columnar boundary of each radial chamber, and also by the ridge of similar tissue on each face of the first pair of mesenteries (fig. 19). And in none of the polyps has the disorganization proceeded so far that the central cavity extends to the aboral region; but the process has progressed further at the oral extremity, whence the hollow tentacles arise.

All the preparations reveal, from the beginning, only a thin epithelium on the three pairs of shorter mesenteries, except towards their connection with the column and with the archenteron, where the layer joins that of the column-wall.

As growth continues the columnar intermesenterial ridges must also become further diminished until the unilaminar epithelium characteristic of the adult polyp is obtained throughout, but the larvæ only present stages towards such a condition. There is every indication that it is the limiting layer of the larval spaces, and not the vacuolated tissue, which persists and con-

stitutes the lining of the adult cavity. In fig. 19, *e, f, g, h*, the limiting-layer appears, as it were, creeping round the ridges still remaining, and thus separating them for disintegration.

The original cœlomic spaces in connection with each radial division, whether above or below the œsophageal region, enlarge as the vacuolated tissue disappears and as the polyps increase in size, and ultimately become the endocœles and exocœles of the adult. These latter are thus shown to have their origin in primary spaces connected with an archenteron, exactly as occurs in the formation of the cœlome in the higher Metazoa, except that partial disorganization supervening, the spaces are never cut off from the central chamber.

In all the larvæ free zooxanthellæ and fragments of the disorganized tissue occur in the gastro-cœlomic cavity. It seems likely that these are ultimately expelled through the mouth of the polyp. I did not observe such in *Lebrunia*; but in *Aulactinia* and other embryos of about the same stage I have watched extrusions of this character going on from the interior; small irregular masses of mucus-like matter, mixed with what seemed to be yolk-particles and zooxanthellæ, would at times be passed out through the oral aperture.

The mesenterial filaments along the free edge of the mesenteries probably represent a divided digestive tube. In which case the space central to the mesenteries, the result of the disintegration, will be gastric, and the peripheral portion of the internal cavity will be cœlomic. Hence the term "gastro-cœlomic" more nearly expresses the true morphological conception of the whole of the internal cavity of the Scyphozoa than either "cœlenteron" or "gastro-vascular cavity."

It follows that the entire imperfectly-chambered internal cavity of the adult *Lebrunia* is ontogenetically both cœlomic and gastric, and is a secondary formation having its origin in two very different phenomena:—Firstly, in a primary system of radiating, archenteric diverticula or cœlomic spaces; and secondly, in the disintegration of a primary, undifferentiated tissue. The former gives rise to the mesenterial chambers, distinct from one another in the œsophageal region, but imperfect below; the latter gives origin to the space (gastric) central to the free edge of the mesenteries, and results in the imperfect character of the mesenterial chambers below the

œsophagus. The greater part of the limiting layer of the spaces persists as the unilaminar epithelium of the gastro-cœlomic cavity of the adult.

4. *Mesenteries.*

Eight mesenteries are present in each stage examined, all perfect in the upper œsophageal region; but only two, the sulco-lateral pair, remain united as far as the lower edge of the œsophagus. All may extend to the aboral termination of the internal cavity, but the sulcular directives sometimes cease a little in advance of the others. The four pairs subdivide the upper œsophageal region into eight chambers, four larger alternating with four slightly smaller, arranged so as to present a perfectly tetrameral, radial symmetry (Pl. 19. fig. 16), in correspondence with that of the tentacles on their first appearance. As the three pairs become free the transverse sections assume a distinctly bilateral symmetry. In their free condition the sulco-laterals continue for a short distance still larger than the rest, but below all the eight are practically equal, and very short in their centripetal extent.

It is remarkable that no increase in the number of mesenteries takes place between the earliest and the latest larvæ, representing a period of about five days. This is in harmony with the numerical condition of the tentacles, but the development of the mesenteries precedes that of the tentacles in all known cases.

In some examples the two sulcar directives, in the proximal region, become united along their free edges.

The mesogloea of the mesenteries is usually broad at its origin in the column-wall, but is extremely thin beyond. In the earliest stages traces of muscular elements are indicated only in the basilar region, but later, transverse sections of very delicate longitudinal fibrils are seen along one face, just sufficiently well-developed to enable the paired arrangement of the mesenteries to be established (fig. 16). This follows the usual order, which is the same as that in *Edwardsia*, namely, the retractor muscles on the directives are on the faces of the mesenteries turned away from one another, while in the two lateral pairs they are on the faces turned towards one of the pair of directives which, by this means, if by no other, can be distinguished as the sulcar directives.

5. *Mesenterial Filaments.*

Mesenterial filaments are apparently undeveloped in the youngest larvæ, in which the whole of the vacuolated tissue is intact. In the earliest stages, however, in which disorganization is in progress, a filament occurs on the first pair of mesenteries, the sulco-lateral. These mesenteries, as already described, remain connected with the œsophagus as far as its lower termination, are much larger than the three other pairs, and are very prominent objects in transverse sections below the œsophagus (Pl. 19. figs. 19, 21).

Of the filament only the middle Drüsenstreif or glandular streak is yet formed. This structure stands out very conspicuously in sections stained in carmine, by reason of the deeply-staining character of its numerous close, oval nuclei, while the free surface is also strongly ciliated. Long, narrow nematocysts, similar to those in the superficial ectoderm and œsophageal lining, occur here and there in different stages of development, and occasionally granular gland-cells can be distinguished.

The filamental tissue extends for some distance down the edge of the mesenteries, but ceases before the aboral termination is reached. Although probably a matter of no particular significance, the filament during these early stages is found to be rarely equally developed on each of the two mesenteries, and generally terminates on one at a level different from that of the other.

In one larva sectionized transversely, the sulcular and sulculo-lateral mesenteries, in addition to the sulco-laterals, remain connected with the œsophagus as far as its aboral ending, and throughout their middle free course are proportionately larger than in other larvæ and also than the sulcar directives. The epithelium on each face is swollen a little, and towards the free edge stains more intensely than elsewhere, indicating that mesenterial filaments are in process of development.

While in the oldest extruded larvæ, and in all the non-extruded specimens (fig. 21), the filamental tissue is in absolute continuity with the similarly deeply-staining lining of the œsophagus or archenteron, a break occurs in earlier stages of the first series, where disintegration has just been set up.

A distinct bridge of unmodified tissue is seen to intervene between the œsophageal lining and the portion of the filament

already developed below. This is clearly shown in fig. 22, representing the centripetal, swollen portion of the sulco-lateral pair of mesenteries of an extruded larva of intermediate age. The section is taken transversely a little below the gullet. At this level the mesentery to the left presents the beginnings of a filament at its free edge, easily distinguished by the oval, deeply-staining, closely-arranged nuclei and fringe of cilia; the mesentery to the right possesses only unmodified epithelium. Only a few sections lower, however, the filament begins to appear on the right mesentery also, and still lower is nearly as strongly developed on both, as shown in fig. 19, taken from a non-extruded larva. Such a separation between the filaments and œsophageal lining occurs in several larvæ of which I possess transverse sections, and also in one longitudinal series.

Any hiatus, however, is of a very temporary character. For in other early stages the filamental tissue already starts directly from the point at which the mesentery severs its connection with the œsophagus, at first very feebly developed, but becoming stronger below. Later, it is fully developed along the whole of its extent.

In this connection the outward and upward continuation of the archenteric or œsophageal lining which takes place at the aboral termination of the œsophagus must be referred to (figs. 17, 18, 21). Prof. H. V. Wilson (1888) found very pronounced reflections in the early stages of the development of the coral *Manicina areolata*. These push away the endoderm of the cœlenteric surface of the stomodæum, and Wilson considers them to be there concerned with the formation of the filaments, except those belonging to the first pair of mesenteries. These originated as direct downgrowths along the column-wall, to the mesogloea of which the stomodæum at an early stage is apposed.

Prof. McMurrich (1891, p. 320, pl. xiii. fig. 17) also describes and figures a reflection at one end of the stomodæum of the larva of *Rhodactis Sancti-Thomæ*.

In several cases I obtain an appearance closely resembling that given by McMurrich; and on following it down, section by section, the deeply-staining tissue is seen to enlarge until ultimately it extends all round the œsophagus, with the exception of the two points from which the first pair of mesenteries are given off (fig. 18). At these it passes along the edge of the mesenteries.

When the sections are perfectly horizontal the reflection at first is equally developed all round, except at the two points mentioned, and is continued above in four distinct bands (fig. 17). The extent of the reflection in the non-extruded larvæ (fig. 21) should be compared with the condition before and after disintegration in the others (figs. 11, 22).

The sections of *Lebrunia* prove that such a condition as that figured by McMurrich—the stomodæum open at one end and the lips partly turned back, and with a free portion of the lining reflected outside the opposite end—is probably due to an obliquity in the sections to the vertical axis of the larva, but it would, of course, also be brought about if the stomodæum terminated at one end earlier than at the other.

The reflection has the significance of constituting the point of continuity between the œsophageal lining and the mesenterial filaments, and occurs also in the adult condition of most Zoantharia.

At the present time one of the most important problems in Actinozoan morphology concerns the origin, from one or other of the two embryonic layers, of the mesenterial filaments. The facts observed in every case are as follows:—Histologically the lining of the œsophagus very closely, though perhaps never completely, resembles the mesenterial filaments; and in the perfect mesenteries of all adult polyps the two are in absolute continuity. In so far as the filaments resemble the stomodæal lining do they differ from the ordinary epithelium of the gastro-cœlomic cavity; everywhere they offer a very strong histological contrast to the latter.

Embryological evidence is here of the greatest value. From this standpoint the question has been approached by Prof. E. B. Wilson (1884) for the Alcyonaria, by Prof. H. V. Wilson for the Madreporaria (1888), and by Prof. McMurrich (1891) and others for the Actiniaria. In his paper on "The Mesenterial Filaments of the Alcyonaria," the first mentioned investigator arrives at the conclusion that the filaments of the two dorsal mesenteries in that group are ectodermal derivatives, that is, downgrowths of the lining of the stomodæum, and are homologous with the Flimmerstreifen or ciliated streaks of the Actiniaria; while the six ventral filaments are endodermal in origin, and correspond with the Drüsenstreifen of the Actinarian filament.

The former E. B. Wilson proves to be specially circulatory in function, while the latter are digestive. Studying the West-Indian coral *Manicina*, in which only the Drüsenstreif is developed, H. V. Wilson found that the filament of the first pair of mesenteries arises as a downgrowth of the stomodæal ectoderm, and the later ones from upward reflections of the same layer. He homologizes the simple Madreporarian filament with the whole of the trilobed Actinian filament. From his researches on *Aulactinia* and *Rhodactis* McMurrich is inclined to agree with E. B. Wilson, and to regard the Drüsenstreif as endodermal and the Flimmerstreifen as ectodermal in origin. The sections of *Aulactinia* revealed a bridge of unmodified endodermal tissue between the early filament and the stomodæal ectoderm, but the results with *Rhodactis* were not so conclusive, although representing earlier stages.

In this strictly limited aspect of the problem the evidence from *Lebrunia* at first sight appears incontrovertible. In having the four pairs of mesenteries already developed, along with a nearly solid interior, the larvæ present conditions very different from those studied by the previous investigators. As already described, no filament is discernible before the gastro-vascular cavity of the adult has begun to be established. And for the next early larvæ, the first portion of the free mesentery in the case of the sulco-lateral pair of mesenteries possesses only unmodified endoderm at its free edge, while a filament is well developed below. It is on evidence precisely of this character that E. B. Wilson and McMurrich affirm the endodermal origin, in the former case, of the six ventral filaments of the Alcyonaria, and, in the latter, of the median streak of the Actiniaria.

Regarding as I do the lower region of the œsophagus in *Lebrunia* as a portion of the archenteron and therefore its lining as endoderm, the significance of its primary relationship with the mesenterial filaments becomes altered from that understood by the writers just mentioned.

From such conditions as those revealed in fig. 21, before any ectodermal invagination appears, it is clear that the archenteric endoderm and the filamental tissue are morphologically one and the same.

I venture to think that in *Lebrunia* the temporary discontinuity in the extruded larvæ between the œsophageal lining and

the developing filaments is a condition of no morphological importance, perhaps due only to the readjustment of the relations between the œsophagus and mesenteries consequent upon the disorganization of the central tissue and the formation of the oral aperture. Any subsequent discontinuity in such a larva as that from which fig. 21 is taken would clearly have no bearing on the morphological value of the filaments.

From the details revealed by the larva of *Lebrunia*, I consider that we are justified in regarding the simple filament of the Madreporaria and Alcyonaria, and the glandular streak of the trilobed filament of the Actiniaria, as representing a continuation of the enteron; a relationship already suggested by other workers (p. 307).

The fact that no such break in continuity as that referred to has ever been observed between the œsophageal epithelium and the lateral or ciliated streaks of the trilobed Actiniarian filament, has led E. B. Wilson and McMurrich to regard these as ectodermal downgrowths from the stomodæal walls, and in this they are followed by most writers on the Actinozoa. My results, however, incline me to the opinion of H. V. Wilson, namely, that the simple Madreporarian filament is homologous with the complex Actinian filament.

Ontogenetically the Flimmerstreifen appear later than the Drüsenstreif, and, at any rate in *Lebrunia*, after the continuity of the latter with the œsophagus has been established. They are always highly specialized structures in that the constituents are wholly columnar ciliated cells, without an admixture of gland-cells and cnidoblasts, thus differing histologically from the œsophageal lining or median streak of the filament. There is little doubt that they are, like the dorsal filaments of the Alcyonaria, special circulatory organs. Usually they are most strongly developed in colonial Actiniaria, such as the Zoanthidæ. The so-called "Reflected Ectoderm" of Haddon (1891, p. 619) met with in this family must, in all probability, be looked upon as a strongly developed portion of the ciliated streak.

To anticipate results yet to be published, I find that along the two sides of the simple filament of the West-Indian species of *Madrepora* a very characteristic structure is developed, in no way histologically distinguishable from the Flimmerstreifen of the Actiniæ.

Such an occurrence in a Perforate coral, in which the circulatory system is very extensive and complex, seems to afford strong evidence for regarding the single filament as the homologue of the whole of the trilobed filament, and consequently for its origin as a whole from one and the same embryonic layer.

In the adult *Lebrunia* the ciliated streaks are strongly developed and continuous with the lining of the œsophagus at its inner termination.

IV. RELATIONS OF THE TENTACLES AND MESENTERIES.

The origin of the different tentacles in relation to the mesenterial chambers discloses some unexpected conditions. And firstly a comparison may be instituted between the time of appearance of the tentacles as external organs of the polyp, and the stage reached in the development of the internal mesenteries and their corresponding chambers.

Though the first eight mesenteries in all Zoantharia yet investigated develop successively in pairs, the early tentacles rarely do so. Lacaze-Duthiers, in his classic investigations already referred to, found the tentacles to appear in *Actinia equina* during the stage in which eight mesenteries were present, one from each mesenterial chamber, as is also the case in *Lebrunia*. Von Koch (1897) apparently found twelve tentacles to appear simultaneously in *Caryophyllia cyathus*, at a stage when twelve mesenteries were developed, eight only of which were perfect. In Haddon's newly-hatched larvæ of *Euphyllia* no tentacles, however, were developed, although six pairs of mesenteries were present, three pairs of which possessed filaments.

On the other hand, both McMurrich and van Beneden found that in the Cerianthid *Arachnactis* the appearance in pairs of the tentacles follows closely upon that of the formation of the mesenterial chambers. But, in consequence of the stomodæum extending right across the cœlenteron, from wall to wall, at the stage of development characterized by the presence of two, or perhaps three, pairs of lateral tentacles, there exists no trace of any median chambers, and it is only when these have been formed that a median tentacle appears. In this case it is the ventral tentacle; a median dorsal never occurs, the region being

one of apparently continuous growth in pairs of the tentacles and mesenteries.

From the few examples given there is evidently little or no connection to be expected between the stage of internal development and the appearance of the tentacles.

In viviparous polyps the formation of the tentacles rarely takes place until the larvæ are set free, whereas the internal development may have proceeded to almost any degree, though apparently not often beyond the *Edwardsia*-stage. Yet in newly-hatched larvæ of *Aulactinia* I found examples with six tentacles already protruding.

The relation of the axis of symmetry of the tentacles in their bilateral stage with that of the mesenteries may now be considered.

In *Actinia equina* Lacaze-Duthiers found the first and largest tentacle to arise from the sulcular endocœle, a smaller and opposite from the sulcar endocœle, and the three lateral pairs, varying somewhat in size, from the lateral mesenterial chambers. The sagittal axis of the tentacles, therefore, is the same as the axis of symmetry of the paired mesenteries, a relationship which would naturally be expected. The longer axis of the stomodæum is also in the same plane. The figures of McMurrich and van Beneden show that in *Arachnactis* the plane of symmetry of the tentacles and of the mesenteric chambers likewise coincide, and von Koch represents the same relations for *Caryophyllia cyathus*.

In one late larva of *Lebrunia*, in which a complete series of transverse sections enabled these relationships to be followed from one end to the other, a different relationship was encountered. This is represented in Pl. 19. figs. 23-25.

The first section (fig. 23), passing through the basal tentacular region, exhibits the relative sizes of the tentacles such as has already been described among the external characters for the bilateral stage. Sections in advance of this leave no doubt as to the correctness of the dorso-ventral relations here indicated. The longer axis of the oval stomodæum is in a plane at right angles to that of the median axis of the tentacles. Fig. 24, taken from a section through the middle stomodæal region, reveals the same bilateral arrangement of the tentacles, but the dorso-lateral tentacles (*f*, *h*) are now comparatively larger than before on account of their relatively lower origin in the polyp.

Under a high magnification the very delicate retractor-muscle fibres on the mesenteries can be made out, enabling the two pairs of directives (III., III. ; IV., IV.) to be determined. These are found to be arranged about an axis ($a-e$) at right angles to the median axis of the tentacles ($g-e$). I have represented the cut ends of the muscular fibrils in the figure, although they could not be discerned at such a low magnification as that given.

The next figure is from a section a little below the stomodæal region, and, although no trace of any tentacles occurs, the section follows the others in regular sequence without any disturbance of the axes. The larva was sectionized in one continuous ribbon and mounted accordingly. As in the previous figure, the sulco-sulcular plane of the larva ($a-e$) is at right angles to what would be the median plane of the tentacles ($g-e$); in other words, the two median lateral tentacles communicate the one with the sulcar (a) and the other with the sulcular endocœle (e), while the two tentacles in the dorso-ventral plane communicate each with a median mesenterial space (c, g).

Another condition is disclosed by the slightly flattened larva from which figs. 26-28 are taken. The series indicates that on the left side the small tentacle next the large dorsal tentacle (f) communicates with the sulcular endocœle (e), and the small tentacle (a) on the right side, next the ventral (b), communicates with the sulcar endocœle (a), so that the median axis of the tentacles ($f-b$) is in a plane oblique to the sulco-sulcular axis of the mesenteries ($a-e$). Here, again, the longer axis of the œsophagus is in the same plane as the sulco-sulcular plane of the mesenteries.

A third larva was in the same condition as the first example described—the median axis of the tentacles at right angles to the axis of symmetry of the mesenteries. And, yet again, a fourth example, traced later, revealed the same oblique relationships as the second here recorded.

In every case the longer axis of the œsophagus coincided with the axis of symmetry of the pairs of mesenteries, not with that of the tentacles.

It is very evident, therefore, from these four cases, that the symmetry of the two sets of organs—tentacles and mesenteries—is independent in the bilateral stage of the larva. It may

perhaps be explained as a result of the late formation of the cœlenteric cavity, of the assumption of the bilateral stage of the tentacles before any decided internal bilateral symmetry has been established in the upper tentacular region, the nearly solid interior having no influence on the method of grouping of the tentacular outgrowths.

Where, as in *Arachnactis*, the outgrowth of the tentacles closely follows the production of mesenterial spaces, it is obvious that the two must be directly related, and that the external symmetry will be moulded upon the internal. Also in the species studied by Lacaze-Duthiers and others, where the cœlenteric chambers were formed in advance of the tentacles, the internal symmetry first assumed would be likely to impress itself upon the external organs arising later.

The irregularity in *Lebrunia* is probably rectified in the subsequent rearrangement of the tentacles in hexamerous cycles, for, in the numerous adult specimens I have examined, the tentacles, œsophageal axis, and mesenteries exhibit the relationships usual in the Hexactiniæ.

V. CONCLUSIONS.

From the foregoing account it is obvious that the larva of *Lebrunia coralligens* presents us with very unexpected conditions in Scyphozoan development; and this not alone in any one particular organ, but in almost every essential structure. The early tetrameral symmetry, followed by a bilateral phase, and that again by the hexamerous adult; the system of ciliated cœlomic spaces connected with a closed archenteron, all embedded in a mass of undifferentiated tissue; the formation of the œsophagus by the breaking down of the floor of an ectodermal invagination in association with an archenteric tube; and the origin of the adult gastro-cœlomic cavity from a primary cœlome and disintegration of the tissues, are all unique characteristics.

The species seems to retain to a late period certain ancestral characters which in other forms are either passed over or disappear very early, so that other features dependent upon their presence are never exhibited. Thus, were the vacuolated tissue insufficiently developed, or to disappear early, we should have no clear evidence of a distinct larval cœlome.

Some of the facts observed in the early larvæ appear to obtain

their full significance only from a comparison with the tetrameral Scyphomedusæ. Commenting upon the connection of this group with the Zoantharia Haddon, ten years ago (1889), wrote:—“The relationship of the Hydra-tuba and Scyphostoma stages of the Scyphomedusæ (Acalephæ) to the Zoantharia is now generally admitted, indeed a group (Tæniolata) has been erected by Professor E. Hæckel to include them both. Later Professor A. Götte has similarly proposed the term Scyphozoa for the same assemblage, but including the Ctenophora, as opposed to the remaining Cœlenterata or Hydrozoa. The Scyphostoma have an œsophagus lined by ectoderm (Stomodæum), four glandular mesenteries, the edges of which are true craspeda, and serve to digest food; in their upper portion nematocysts are present. The four tentacles are afterwards increased to eight, and finally to sixteen. It is especially noteworthy that at first there are only two tentacles: probably this is a reminiscence of a remote ancestor. The widespread occurrence of a symmetry of four amongst the larvæ of the Scyphozoa is very suggestive.”

Discussing the Phylogeny of the Actinozoa McMurrich (1891 *a*, p. 149), two years later, also remarked:—“As regards the relations of the Actinozoa to other Cœlenterates, there is little to be said; the majority of authors who have committed themselves upon the subject, agree in tracing the Actinozoan stem back to a form similar to the *Scyphistoma*. The evidence we have seems to point in that direction; but it must be acknowledged that it is exceedingly scanty, and there are many points of difference between any *Scyphistoma* of which we have a description and the simplest Actinozoa. It seems probable, however, that the Actinozoa are to be traced back to an ancestor possessing only four mesenteries. The occurrence of an octamer symmetry in the simplest Actinozoa seems to point in that direction, as well as the fact that, in the development of the Hexactiniæ, the stage with four mesenteries seems to mark an epoch, much less distinct, however, than that indicated at the close of the *Edwardsia* stage.”

The tetrameral symmetry of the *Lebrunia* larva, perfect as regards the tentacles, and the mesenteries and cœlomic diverticula of the upper archenteric region, seems to be explicable only on such a throwing back of the ancestry of the Zoantharia. The two alternating series of four tentacles exactly recall the eight-

armed stage passed through by most Scyphostoma, and the arrangement of the four canals, with the circumferential sinus terminating in eight divisions bifurcated at the end, resembles a gastro-vascular system such as that of the Ephyra.

Though in the particular case of *Lebrunia* the eight tentacles develop simultaneously, it does not follow that they may not have had an ancestry in which they arose in pairs, as happens in the Scyphostoma. For there is evidence that such fundamental structures as the primary mesenteries develop successively in pairs, as is the case in all other Zoantharia. The two constituting the fourth pair (sulcular directives) in most cases disappear at the aboral end before the others, and in every case the first pair (sulco-lateral) are larger than the others, and are the only ones which bear mesenterial filaments.

The results appear to justify to a greater degree than has before been possible Hæckel's and Götte's union of the Scyphomedusæ and Actinozoa under the term Tæniolata or Scyphozoa; a relationship first rendered probable by the discovery of the ectodermal character of the stomodæal lining of the former, and the presence of mesenteries and gastric filaments. The strong objection founded on the tetrameral character of the Scyphomedusæ, as compared with the hexamerous nature of the Actiniaria, disappears on the demonstration that the larvæ of the latter may pass through a tetrameral stage, directly comparable with that permanent in the former.

Further, where the transition from one stage to the other can be followed in the ontogeny of a single form, we have another to the many objections against the separation of the Tetracorallia or Rugosa from the Hexacorallia. There can be no fundamental distinction on the ground of symmetry alone.

The very marked arrest of the mesenterial and tentacular development in *Lebrunia* at a tetrameral or octamerous stage, and the fact that such occurs to a greater or less degree in apparently all other Zoantharia (*Edwardsia*-stage), suggest this as either a permanent stage or as a starting-point for various modifications, and emphasizes with how little reliability adult structure can be accepted as evidence of phylogenetic relationship.

The Rugosa and Alcyonaria retain approximately a tetrameral or octamerous type of symmetry, while the Hexacorallia and Actiniaria, by the further addition of two lateral pairs of

mesenteries, give rise to another—the hexamer. Even amongst the Hexactiniæ, however, octamer or tetramer examples may occur; occasionally in such a form as *Aiptasia annulata*, but apparently always in most species of the genus *Corynactis* (Duerden, 1898, p. 649).

McMurrich (1891, p. 311) is inclined to regard the differences of arrangement of the retractor muscles of the mesenteries, such as one sees in the directives of the Aleyonaria and in the Zoantharia, as of secondary importance, in comparison with the order of development and number of mesenteries.

Undoubtedly the character of greatest concern is the occurrence in an Actinian of what appears to be a system of primitive cœlomic spaces connected with a closed archenteron, within an otherwise solid interior. And it remains to be seen what support there is for the views already advanced in regard to such.

Until the earlier stages of the embryo have been obtained, it is impossible to determine the manner in which the conditions have arisen, and therefore to homologize them with certainty with what occurs in other groups. It will be necessary to ascertain whether an actual primary invagination takes place before or after the appearance of the supporting lamella, and if the spaces themselves are primitively formed as evaginations of this, the limiting layer being a direct continuation of its walls; or, whether the spaces originate independently as splittings within the solid tissue, their limiting layer then arising as a modification of the marginal cells, and later entering into communication with the internal end of the archenteron.

The evidence obtainable from the development of other Scyphozoa assists but little in the elucidation of the actual facts presented by *Lebrunia* at the stages under consideration. From the fertilized ovum a blastosphere results, and, according to the accounts of some observers, the two-layered planula is formed by invagination, and, according to others, by delamination. Reviewing all the known cases, McMurrich (1891), in the light of his own results with *Metridium*, comes to the conclusion that, with the probable exceptions of *Pelagia* and *Nausithoë*, in every case the endoderm in the Scyphozoa is produced by delamination; that the results of Kowalewski with *Actinia* (sp. ?) and *Cerianthus*, of Jourdan with *Actinia equina*, as also of Hæckel with the Aleyonarian *Monoxenia*, in that they ascribe the production of

the gastrula, and consequently of the endoderm, to invagination, are a misinterpretation of the appearances.

In the course of development a primitive mouth or blastopore appears to be always formed, and in some instances becomes closed; but in any case the permanent mouth and stomodæum are considered to arise by a later infolding of the ectoderm.

At the conclusion of the delamination in *Metridium* McMurrich (1891, p. 308) observed a slight depression at the posterior pole of the larva, which soon after breaks through, a communication of the interior cavity with the exterior being thus established. His latest stages of this species did not permit of his ascertaining the manner of formation of the stomodæum. A primary mouth, with a later invagination of the two-layered wall to form the stomodæum, is figured by Kowalewsky for *Actinia* (sp.?) and *Cerianthus*, and by Jourdan for *Actinia equina* and apparently for the coral *Balanophyllia* (1884, 'Embryological Monographs,' pls. xi.-xiii.).

In *Aurelia*, Götte found that after the planula settled down an ectodermic invagination is formed, its lower end breaking through, thus establishing a communication of the interior with the exterior and constituting the œsophagus. First two and then four diverticula or gastric pouches of the general cavity are formed and arranged around the œsophagus, and a reflection of the lining of the latter also appears to take place.

I believe it will ultimately be found that the early stages in the development of *Lebrunia* will be better understood by a comparison with what occurs in the Scyphomedusæ than by what happens in the Actinozoa.

In *Lebrunia*, we are confronted with the facts that a stomodæal-like funnel already exists in association with a considerable mesenterial development, and that up to the time of liberation of the larvæ no oral aperture is present, but that this is formed shortly after extrusion.

Can we then, in face of what is already known in Scyphozoan embryology, assume that the first mentioned structure is an endodermal-lined archenteron, the blastopore of which has become and is still closed, and that the later invagination is the one corresponding with that which gives rise to the mouth and ectodermal stomodæum in all other known Scyphozoan larvæ?

Until the study of earlier stages can settle the question

absolutely I can come to no other conclusion, and, of course, the correctness or otherwise of the explanation of many of the other peculiar features is determined thereby. The view has the merit of placing the conditions in strict harmony with what occurs in many *Enterocœla*.

The limiting layer of the larval cœlomic spaces in continuity with the lining of the archenteron must be considered as the equivalent of the wall of the cœlomic pouches or cœlomic splittings of the higher Metazoa. Here it is usually regarded as mesoderm or mesothelium, the latter term being employed in order to distinguish it from the mesoderm—"mesenchyme"—arising by immigration.

The tendency, however, is to regard still as endoderm the walls of all the outgrowths from the archenteron and their derivatives. Thus in the latest important work on the morphology of the Echinoderms, Dr. H. L. Clark (1898) describes as mesoderm only the tissue of mesenchymal origin, and this plays a very insignificant part in the adult structures. Under endoderm he includes all the derivatives of the archenteron and its hydroenterocœl, embracing amongst other structures the lining of the digestive tract with most of the œsophagus; all the muscles of the body-wall and gut; the peritoneal lining of the body-cavity and epithelial covering for the various organs contained in it, as well as the genital organs and their ducts.

Homologizing the limiting layer of the cœlomic pouches in *Lebrunia* with the peritoneal epithelium of the body-cavity of the higher Metazoa, we may, with Clark, still regard it as endoderm, or, following the more usually accepted terminology, speak of it as mesoderm; and, as in all the *Enterocœla*, it gives origin to the principal muscular system and the gonads. The portion adjacent to the column-wall and that covering the two faces of the mesenteries would correspond with the somatic, and the remainder with the splanchnic layer of the higher Metazoa, and it is the former which remains as the epithelial lining of the major part of the adult mesenteric chambers. Below the œsophageal region it is the splanchnic layer which disappears during disintegration, but above, this constitutes the cœlomic lining of the gullet.

What, then, of the vacuolated mass of tissue which probably entirely disappears in the adult? It is the tissue within which

the cœlomic spaces are formed. To continue the comparison with the Triploblastica, may we not regard it as the equivalent of the "mesenchyme" of the higher Metazoa? It is evident that in *Lebrunia* it is little more than a larval "packing-tissue," disappearing as the adult Scyphozoan characteristics are taken on. As already mentioned, however, it probably shares in the formation of the muscular system.

Even though beyond the œsophagus no separate digestive tract with closed walls remains in the adult, there seems little doubt that the mesenterial filaments are to be looked upon as representing an endodermal-lined digestive gut, continuity with the œsophagus being either original or established at a very early stage. As the primary distinctness of the cœlomic pouches has broken down at an exceptionally early stage, so the walls of the enteron come to be represented only by thickened ridges along the free edge of the septa of the cœlome. Or the same result may thus be conversely stated, and perhaps with greater morphological truth, that as the lower portion of the enteron beyond the point at which diverticula are given off is not formed early enough, so the mesenchyme and cœlomic epithelia, which on their part are developed and would have surrounded it, become disintegrated, leading to the imperfect condition of the cœlomic chambers in the adult. It only remains to conceive of the adult mesenteries uniting along their lateral edges and we should have a closed gut as in the higher Metazoa, lined above by the invaginated ectoderm and below by the archenteric endoderm. The mesenterial chambers thus distinct from one another would constitute a true cœlome or body-cavity, exactly as in the œsophageal region and in the Enterocœla. As it is, the Scyphozoa are distinguished by having the lower portion of the enteric system in separate longitudinal bands, its cavity in communication laterally and below with the chambered body-cavity.

Were the explanations here offered to be confirmed, the occurrence in the Scyphozoa of an archenteron with distinct radiating cœlomic diverticula would be recorded for the first time, but the broad relationships of the group with the higher Metazoa thereby implied have been already surmised by various workers.

Prof. E. B. Wilson (1884), in his paper on "The Mesenterial Filaments of the Alcyonaria," devotes a section to the relations

of the Anthozoa to the Enterocœla. Having established, both experimentally and histologically, that the digestive functions of the Aleyonaria are confined to the six ventral mesenterial filaments, he regards the latter as the representatives of the alimentary canal of higher animals, and suggests that "they are not only physiologically but also morphologically the equivalents of the enteron of the Enterocœla"; and continuing, affirms that "morphologically we may regard the radial chambers as diverticula from the primitive enteron."

Van Beneden (1891), from his study of the development of the larval Cerianthid *Arachnactis*, likewise comes to the same conclusion in reference to the mesenteric chambers of the Anthozoa and the cœlomic diverticula of the higher animals. He devotes special attention to a comparison of the origin and arrangement of the mesenteries and their chambers in the Cerianthidæ with paired cœlomic diverticula of the segmented Metazoa.

According to a preliminary notice appearing in 'Nature,' March 2, received when this contribution was nearly completed, Mr. J. Stanley Gardiner, studying a supposed new species of the coral *Cœnopsammia* from Lifu, has also come to practically the same conclusion as Prof. E. B. Wilson in regard to the enteron and mesenterial filaments. The notice contains the pertinent sentence: "It was further contended that the stomodæum together with the mesenterial filaments is homologous with the whole gut of the Triploblastica, and that the so-called endoderm is homologous with the mesoderm. The Actinozoon polyp then must be regarded as a Triploblastic form."

In the larva of *Lebrunia* we appear to have the actual embryological proof of these surmises, founded mostly upon a consideration of the adult anatomy. And it is clearly such a problem as can only be established on embryological grounds.

Whether the larval spaces are derived originally as paired or radiating evaginations of the terminal region of an archenteron, and their walls are then to be regarded as mesothelium or endoderm, or whether they originate as splittings within the solid undifferentiated cell-mass, matters but little. Both processes occur in the higher animals: in some the cœlome originates from endodermic diverticula, *e. g.* Echinodermata, *Amphioxus*; in others from mesoblastic splitting, *e. g.* nearly all Vertebrates.

The main point sought to be established is that the larval spaces of *Lebrunia* represent a paired cœlome embryologically equivalent to that of the higher Metazoa, and, consequently, that the chambers of the adult are the same. For there is no doubt as to the manner in which these latter arise from the primary spaces.

It remains to discuss what support there is otherwise for such a change in conception of the layers and internal cavity of the Scyphozoa.

Prof. J. P. McMurrich, in his most valuable series of "Contributions on the Morphology of the Actinozoa," devotes Part II. (1891) to the development of the Hexactiniæ, and therein describes an almost complete series of stages from the egg to the adult, taking his examples from the genera *Metridium*, *Rhodactis*, and *Aulactinia*. In reviewing all the known cases of early development, he concludes, as already mentioned, that the so-called endoderm of the Actinozoa is derived from the hollow blastula by the process of delamination, not by invagination, the extent of its cellular development being mainly dependent upon the amount of yolk present.

Following partly the results of Metschnikoff, McMurrich regards the process of delamination as a modified form of the more primitive process of immigration. In groups higher than the Cœlenterata the products of immigration, whether from the ectoderm or endoderm or from both, are regarded as mesodermic (*ex.* the "mesenchyme" of Echinoderms). There is little doubt that the internal parenchymatous tissue of the *Lebrunia* larva has arisen by delamination in the same way as in other Actinozoa: hence, if an independent endoderm, as from an archenteric invagination, can be established, there seems no reason why the first-mentioned tissue should not be regarded as the homologue of the mesoderm of higher Metazoa. May we not in *Lebrunia* have "mesenchyme" arising by delamination (in migration), and "mesothelium" (endoderm) from an archenteric invagination, as in the Echinoderms?

To the solid larval stage in the Actinozoa, where segmentation is completed and before the formation of the stomodæum, McMurrich (p. 310) applies the term "Sterrula."

In many Aleyonaria, and apparently in some Madreporaria (*Manicina* and *Balanophyllia*), this is a solid mass of more or less definite cells; whereas in *Metridium*, so far as McMurrich's

embryos allowed the study to be continued, the sterrula was provided with only a comparatively narrow layer of endoderm, the remainder of the cavity being filled with yolk-granules. In the solid sterrula of the *Aleyonaria* the middle cellular tissue early begins to disorganize as the growth of the larva proceeds, giving rise, of course, to the usual cœlenterate gastro-cœlomic cavity with a unilaminar epithelium; while in the other cases it seems that the cœlenteron is produced by the absorption of the yolk, or some of the latter may be extruded through the mouth of the embryo.

The earliest larva of *Lebrunia* I possess has passed beyond the sterrula stage, the mesenteries and the archenteron being already formed. It is in the late stage to which the solid cellular tissue persists, that the species appears to differ from other examples yet recorded. And it would appear to be this entire retention of the central tissue, as compared with its early disappearance or absence in other Scyphozoa, which may enable the morphological conceptions of the other systems to be obtained in such a way as is known for no other species.

Is there any evidence that such a system of diverticula occurs at any stage in other Actinozoa? For it can scarcely be supposed that such an apparently fundamental phenomenon is restricted to an isolated type.

Few Zoantharia larvæ of exactly the same stage as the earliest *Lebrunia* have been minutely described. In some respects, as in the stage reached in the development of the mesenteries, the *Lebrunia* larva is far advanced; but in others—the persistence of the vacuolated tissue and non-formation of oral aperture—it is somewhat early in its development. McMurrich (1891) found in the youngest embryos of *Rhodactis Sancti-Thomæ* that the so-called endoderm-cells completely fill the central cavity, and show little or no arrangement into a definite layer. At the stage, however, where only two mesenteries are present, a well-marked central cavity already existed below the upper region of the body, though the endoderm above was yet solid, no inter-mesenterial cavities having appeared. In this species then the solid endoderm begins to disorganize at a much earlier stage than in *Lebrunia*, in fact before the mesenteries, with which the spaces are associated, are formed. McMurrich's earliest stages of *Aulactinia* possessed eight perfect mesenteries, the first only

being provided with mesenterial filaments. They therefore correspond with the oldest stage in *Lebrunia*. The endoderm, however, had already arranged itself into a somewhat definite layer, but lying scattered about in the body-cavity of the embryo were numerous, somewhat large, cellular elements and yolk-granules.

The Zoanthid larva which van Beneden (1890) identified as closely related to Semper's larva presents three pairs of complete mesenteries and four incomplete pairs, and a very thick endoderm, with small cœlenteric spaces within the stomodæal region. Below, however, a considerable gastro-vascular cavity is formed. The same author (1891) found the larvæ of the Cerianthid *Arachnactis*, at the stage with only one pair of mesenteries and two pairs of tentacles, to possess a cœlenteron fully formed with an endodermal lining of only a single layer of cells. Prof. G. von Koch observed a central cavity in *Gorgonia* and in *Caryophyllia cyathus* (1897) before the formation of any mesenteries or the production of an oral aperture and stomodæum.

In the newly-hatched larva of *Euphyllia rugosa*, Haddon (1890) found three of the twelve pairs of mesenteries already bearing filaments, and alternating with the mesenteries were "large ridge-like vesicular outgrowths from the endoderm." There can be little doubt that, as in *Lebrunia*, these latter are the detached survivors of a more or less solid vacuolated tissue in the earlier stages of the larvæ. Prof. E. L. Mark ("Selections from Embryological Monographs," pl. xii. fig. 32) figures similar inter-mesenterial protrusions, thoroughly vacuolated, in *Edwardsia*. The appearances should be compared with fig. 19 and with the left side of fig. 20 (Pl. 19) in the present paper. The phenomena are remarkably alike. On plate xiii. fig. 15 of the same publication, Prof. Mark reproduces the transverse section of the larva of *Balanophyllia regia* given by E. Jourdan, in which the embryo is still solid, though the central portion is indicated as yolk. Six mesenteries are here shown and the internal yolk seems clearly separated from the endoderm, which latter is still many cells in thickness. The conditions appear to be somewhat comparable with those in fig. 14 (Pl. 18) of *Lebrunia*. I regret exceedingly that, not having Jourdan's original memoir for reference, I can do no more than merely draw attention to the possibility of larval cœlomic spaces being present in such a case. The thick

vacuolated endoderm persistent in *Euphyllia* and *Edwardsia* just mentioned recalls so strongly the conditions in the late larvæ of *Lebrunia*, that it seems not improbable similar diverticula may also have occurred in these species at an earlier stage in their development.

It is evident from all this, that in most Scyphozoa the formation of the gastro-cœlomic cavity of the adult takes place at a much earlier stage than in *Lebrunia*, so that probably no complete and distinct larval cœlomic system is ever formed. This in no way disproves the view here presented. All that can be asserted from the *résumé* just given is that the disorganization to form the secondary body-cavity usually originates at such an early stage that no opportunity exists for the primary enteric and cœlomic system to establish itself. From such conditions as those revealed by *Lebrunia* in fig. 15 (Pl. 19), there seems no reason why at some time a species may not be found in which the archenteron is prolonged centrally beyond the origin of the diverticula, in which case we should have a temporary digestive cavity with closed walls. In this connection one is tempted to recall the ramified digestive tract described by Bourne (1887) as occurring in *Euphyllia*.

The larva of *Lebrunia* is in many respects of an exceptional character. If the interpretation of its tetrameral primary tentacles be correct, it shows that phylogenetically it is, in regard to these organs, at a stage earlier than other Zoantharian larvæ yet described, and perhaps the same may be said of much of its internal condition. No doubt the two sets of phenomena are in some way interdependent.

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EXPLANATION OF THE PLATES.

Reference figures and letters.

The Roman numerals I. to IV. are throughout opposite the four pairs of mesenteries, and also represent respectively the order in which they usually appear in the development of the Zoantharia.

- I. I. Sulco-lateral pair.
II. II. Sulculo-lateral pair.
III. III. Sulcar pair of directive mesenteries.
IV. IV. Sulcular pair of directive mesenteries.

The letters *a-h* correspond with the mesenterial chambers: *a*, sulcar endocœle; *b*, left sulco-lateral chamber; *c*, left median lateral chamber; *d*, left sulculo-lateral chamber = sulcular exocœle; *e*, sulcular endocœle; *f*, right sulculo-lateral chamber = sulcular exocœle; *g*, right median lateral chamber; *h*, right sulco lateral chamber. Both for the mesenteries and the chambers the terminology here adopted must necessarily become slightly altered as other mesenteries appear.

arc.w., wall of archenteron.
cl.gl.c., clear gland-cells.
cœ.s., cœlomic space.
d.nem., developing nematocyst.
cct., ectoderm.
ect.f., floor of ectodermal invagination.
gr.gl.c., granular gland-cells.
l.nem., large nematocyst.
l.lay., limiting layer.

mes.fil., mesenterial filament.
mus.l., muscular layer.
ner.l., nerve-layer.
œs., œsophagus.
or., oral aperture.
s.nem., small nematocyst.
sp.l., supporting lamella.
sup.c., supporting cells.
vc.t., vacuolated tissue.
zoox., zooxanthellæ.

PLATE 18.

Figs. 1-7 are not drawn to any scale; 1-6 are representations of the living larvæ as seen under a low power of the microscope, and 7 as seen with a hand-lens. All the others are from sections, and were drawn with the assistance of a camera.

Fig. 1. The usual form of the freshly-extruded, free-swimming larva.

Fig. 2. A form occasionally assumed.

Fig. 3. The contracted cake-like condition.

Fig. 4. Oral aspect of a free-swimming larva a few hours after extrusion.

Fig. 4 a. Lateral aspect of a larva a few hours after extrusion. The tentacular protuberances are beginning to appear.

Fig. 5. Oral aspect of free-swimming larva.

Fig. 6. The same seen from the side.

Fig. 7. A larva three or four days old. (See Plate 19.)

Fig. 8. Vertical section through the middle region of the column-wall of a non-extruded larva in which the central tissue has already become disorganized. $\times 450$.

Figs. 9-11. Vertical sections through the archenteric region of a larva very shortly after liberation, showing the formation of the oral aperture and œsophagus. $\times 320$.

Fig. 9. Tangential section near the periphery of the archenteric wall. The flattened inturned ectoderm is in close contact with the flattened archenteric wall below. The upper narrow slit indicates the upper outer surface of the floor of the former, and the broad slit below is the central œlomic space, to the right continued peripherally and below.

Fig. 10. Tangential section near the centre. The actual oral aperture appears; the floor of the invaginated ectoderm is convex and produced laterally.

Fig. 11. Radial section. The floor of the invagination and the roof of the archenteron are here broken through and complete communication is established between the interior and exterior. The invaginated ectoderm forms the greater part of the œsophageal wall, but the innermost portion is derived from the archenteric endoderm. The union between the two is indistinguishable, but from other sections it is clear that it occurs about halfway below the lateral indentations.

Figs. 12-14. Transverse sections of a freshly-extruded larva before disorganization is set up. $\times 250$.

Fig. 12. Through the upper archenteric region. The section is taken slightly obliquely to the vertical axis and serves to represent the various

appearances of the cœlomic spaces. *d, e, f, g*, present the successive appearances from above downwards, showing how the single mesenterial space ends in two distinct cornua. Between *a, b* the separating mesentery has broken down and the two chambers are in communication one with the other, and a little lower also with the space in *h*.

Fig. 13. The figure is made up of the appearances presented by several oblique sections through the region of the termination of the archenteron. Four radiating canals communicate with the two cœlomic sinuses, the latter separated by the first pair of mesenteries—sulco-lateral, developed to a greater extent than the three other pairs. The limiting layer of the sinuses is both somatic and splanchnic.

Fig. 14. A little below the archenteric region. The middle of the larva is filled with vacuolated tissue; towards the upper side the cœlomic canals are completely separated one from the other, while on the lower side the last traces of the connections are seen, and to the right the last trace of the sulcar canal.

PLATE 19.

Fig. 15. Vertical radial section of a freshly-extruded larva such as would be obtained along the line *x, y* in fig. 12. $\times 120$.

Figs. 16-20. Successive transverse sections through one of the non-extruded larvæ where disorganization of the central tissue is in progress. The sections are such as would be obtained along the lines 1-1, 2-2, 3-3, 4-4, 5-5, respectively in fig. 21. $\times 120$.

Fig. 16. Section through the upper archenteric region. The mesenterial chambers are founded on a radial plan, four large and four small.

Fig. 17. Section towards the termination of the archenteron. In the ventral or sulcar sinus the splanchnic portion of the central tissue shows two separate regions of more deeply-staining tissue continuous with the archenteric lining and with the limiting layer, while in the sulcular sinus the reflected ectoderm is an almost continuous limiting layer.

Fig. 18. Section nearer the termination of the archenteron than in the last figure. Owing to its reflection the lining of the archenteron is cut through twice. The lumen of the archenteron is very small and circular. $\times 320$.

Fig. 19. Section below the archenteron. The splanchnic portion of the limiting layer and the tissue enclosed by it have become disorganized, and only loose fragments remain. The somatic layer and the vacuolated tissue between it and the supporting lamella are as yet unchanged.

- Fig. 20. Section towards the aboral region. Stages in the disorganization of the central tissue are represented.
- Fig. 21. Vertical section through a larva of the same stage, such as would be obtained along the lines I-x, x-I in fig. 19. The section passing through the pair of mesenterial filaments shows their continuity with the lining of the archenteron.
- Fig. 22. Transverse section through the free edge of the sulco-lateral pair of mesenteries of a larva one or two days old, taken a little below the œsophagus. The mesentery to the left shows the beginning of the formation of the mesenterial filaments, while that to the right is as yet unaltered. A few sections lower the filament appears strongly developed on each. $\times 320$.
- Figs. 23-25. Transverse sections selected at different levels from a complete series through a larva several days old, showing the relation of the plane of symmetry of the tentacles to the sulco-sulcular plane of the larva. $\times 50$.
- Fig. 23. Section through the tentacular region and the œsophagus. The tentacles towards their origin are in the same bilateral relation as in fig. 7. The mesenterial chambers are further developed than in any previous section represented. The larger axis of the œsophagus is at right angles to the dorso-ventral axis of the tentacles.
- Fig. 24. Section towards the lower end of the œsophagus representing still the same relations. The sulco-sulcular axis of the mesenteries (*a-c*) and the longer diameter of the œsophagus are at right angles to the axis of symmetry of the tentacles (*g-c*).
- Fig. 25. Section below the œsophageal region and the tentacular prominences. The axes are in the same relation as in the two previous figures. The axis of symmetry of the mesenteries is at right angles to that corresponding with the dorso-ventral axis of the tentacles.
- Figs. 26-28. Transverse sections through a slightly compressed larva of about the same age as the former. The series show that the sulco-sulcular plane of the larva (*a-c*) is oblique to the dorso-ventral plane of the tentacles (*f, b*). $\times 50$.
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J. P. Edwards del.
A. R. Hammond lith.

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